

# Relationships between daytime carbon dioxide uptake and absorbed photosynthetically active radiation for three different mountain/plains ecosystems

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[1] Mean midday values of eddy covariance CO<sub>2</sub> flux and absorbed photosynthetically active radiation (APAR), derived from solar irradiance and normalized difference vegetation index (NDVI), were measured from May to September 1999 with an aircraft at 60–90 m above ground level over three different ecosystems dominated by native plant species in southeastern Wyoming (mixed conifer forest, mixed short-grass prairie, and sagebrush shrubland). The midday net CO<sub>2</sub> uptake at each site followed seasonal trends, with summer values occurring later over the forest than over the other sites. At the landscape scale, linear relationships were observed between CO<sub>2</sub> uptake and APAR for the grassland and shrubland, with increasing APAR leading to increasing CO<sub>2</sub> uptake. Over the forest, however, the CO<sub>2</sub> uptake was only weakly related to APAR, but an additional linear relationship with infrared surface temperature (T<sub>IR</sub>) implied that respiration may have been more important than APAR in determining net CO<sub>2</sub> uptake by the forest. The regression slope for net CO<sub>2</sub> uptake versus APAR for the grassland data agreed with those from other observations.

**INDEX TERMS:** 0315 Atmospheric Composition and Structure: Biosphere/atmosphere interactions; 1610 Global Change: Atmosphere (0315, 0325); 1615 Global Change: Biogeochemical processes (4805); 1640 Global Change: Remote sensing; 3307 Meteorology and Atmospheric Dynamics: Boundary layer processes; **KEYWORDS:** CO<sub>2</sub> flux, absorbed PAR, carbon cycle, remote sensing, airborne flux measurements

## 1. Introduction

[2] Increasing evidence of global warming and consequent prognoses of ecological impacts [Sugden and Stone, 2001], along with recent evidence reaffirming the role of increasing atmospheric CO<sub>2</sub> as the primary driving force for global warming [Shackleton, 2000; Levitus *et al.*, 2001], highlight the need to monitor plant cover and corresponding surface CO<sub>2</sub> uptake on a large scale. Such data will aid in more accurate estimates of regional and global carbon budgets and, ultimately, more accurate predictions of carbon source-sink relationships and atmospheric CO<sub>2</sub> concentrations. Satellite measurements combined with models of terrestrial net primary productivity provide one method for such long-term monitoring at regional and global scales, especially when related to in situ measurements of surface

processes. In the present study, relationships between daytime net CO<sub>2</sub> uptake and absorbed photosynthetically active radiation (APAR) were examined using aircraft measurements from late spring to early fall for three different landscapes dominated by native plant species in southeastern Wyoming (mixed conifer forest, mixed-grass prairie, and sagebrush shrubland). Using analogs based on similarity to the Wyoming sites and drawing from the United States Geological Survey North American Land Cover Characteristics Database [Brown *et al.*, 1999], these types of conifer forest, mixed grassland, and shrubland steppe represent about 4.1, 12.8, and 6.3% of the contiguous 48-state land cover, respectively.

[3] In the present study both the CO<sub>2</sub> uptake and APAR were derived from aircraft measurements, using eddy covariance for the uptake (net flux toward the surface) and calculating APAR from incident solar irradiance and the normalized difference vegetation index (NDVI). Direct correlations between CO<sub>2</sub> uptake and several vegetation indices have been studied in other airborne experiments [Desjardins *et al.*, 1992a; Ogunjemiyo and Schuepp, 1997; Sellers *et al.*, 1992, 1997; Cihlar *et al.*, 1992]. Various models incorporating the dependence of CO<sub>2</sub> uptake on APAR have been described and compared with experimental results, primarily for surface measurements with correspondingly small footprints [e.g., Ruimy *et al.*, 1994, 1995; Liu *et al.*, 1999; Hunt *et al.*, 1996]. The results of the present study were based on aircraft measurements with

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**Table 1.** Mean Annual Precipitation, Flight Dates, and Number of Low-Level Passes for Each Date, and Dominant Species for Each Site

Site	Average Annual Precipitation, cm	Flight Dates (1999) and Number of Passes for Each Date <sup>a</sup>	Dominant Species
Grassland	37.8	May 19 (2), 21 (4); June 1 (4), 22 (4), 23 (10); July 21 (2), 23 (4); Sept. 22 (4), 23 (12)	<i>Stipa comata</i> , <i>Bouteloua gracilis</i> , <i>Artemisia frigida</i> , <i>Agropyron smithii</i>
Shrubland	26.3	May 24 (4), 25 (4); June 2 (5), 14 (4), 18 (4); July 12 (4), 13 (4); Sept. 15 (4), 16 (16), 29 (6)	<i>Artemisia tridentata</i> ssp. <i>wyomingensis</i> , <i>Agropyron spicatum</i> <i>Stipa comata</i> , <i>Koeleria pyramidata</i>
Forest	40.2	May 26 (4); June 3 (4), 17 (4), 21 (3); July 10 (4); Sept. 17 (6), 21 (6)	<i>Pinus contorta</i> , <i>Picea englemannii</i> , <i>Abies lasiocarpa</i>

<sup>a</sup> The number in parentheses after each flight date is the number of low-level aircraft passes used to calculate the average CO<sub>2</sub> uptake, APAR, etc., used in the plots and regression analyses of sections 3 and 4.

substantially larger footprints over sites with plant cover that is quite uniform in species composition, thus presenting an opportunity to evaluate the uptake-APAR relationships at larger scales.

## 2. Experimental Methods

### 2.1. Site Selection and Description

[4] The three sites monitored in this study were chosen for maximum homogeneity of plant cover along flight lines of at least 19 km, using existing plant surveys from Landsat Thematic Mapper (TM) images and airborne photography [Driese *et al.*, 1996]. Table 1 lists the mean annual precipitation [Martner, 1986], flight dates, number of low-level aircraft passes for each date, and dominant plant species for each site. The sites were also chosen to allow low-level aircraft access. Table 2 lists terrain information for each flight line, including the line length, orientation, mean elevation, maximum change in elevation (difference between highest and lowest points), mean slope (in the direction given in column 3), and the general aspect and aspect-direction slope of the larger area traversed by the flight line. The mean slopes (column 6) were obtained from linear regressions of the surface elevation profiles along the flight lines.

### 2.2. Flight Patterns and Schedules

[5] Airborne eddy covariance, solar irradiance, and NDVI measurements were made with the University of Wyoming King Air research aircraft (operated as a national facility under a cooperative agreement with the National Science Foundation) during repeated, level passes along

transects over each site at altitudes of about 60–90 m above ground level (agl). The aircraft was navigated along each transect with help from a cockpit Global Positioning System receiver (Trimble Navigation Model 2000, Sunnyvale, California). With a GPS horizontal position accuracy of  $\pm 0.1$  km, and allowing for navigation error, the flight line locations were repeatable to within about  $\pm 0.25$  km. All aircraft flights were initiated middle to late morning under minimum cloud cover, ensuring a well-developed convective boundary layer and allowing measurements to be completed before the onset of widespread convective cloud formation characteristic of afternoon periods. Thus, the net CO<sub>2</sub> uptake values used in this analysis were for middle to late morning atmospheric and ecosystem conditions at each site.

### 2.3. Instrumentation and Calculations

[6] Data for the eddy-covariance calculations (3-D air motion, air temperature, air pressure, water vapor concentration, and CO<sub>2</sub> concentration) were gathered with the same instruments described by Dobosy *et al.* [1997]. Updates from that configuration included (1) using reference gas from an on-board cylinder for the infrared gas analyzer (LICOR 6262, Lincoln, Nebraska), rather than recirculating chemically scrubbed air and (2) a new data system which sampled analog signals at 100 Hz after anti-alias, low-pass filtering with a filter cutoff frequency of 20 Hz. The eddy-covariance-related variables were resampled and archived at 20 Hz for analysis.

[7] Aircraft radiometer data, which included solar irradiance (Eppley PSP pyranometer, Newport, Rhode Island), surface IR temperature (Heimann KT-19.85, 9.6–11.5  $\mu$ m;

**Table 2.** Line Length, Line Orientation, and Terrain Information for the Aircraft Flight Line at Each Site

Site	Flight Line Length, km	Flight Line Orientation <sup>a</sup>	Mean Elevation, m	Maximum Elevation Range, m	Mean Slope, %	Aspect <sup>b</sup>	Mean Aspect Slope, %
Forest	19.3	168°	2755	240	−0.24	S	−2.0
Grassland	24.9	67°	1699	150	−0.57	WSW	−1.3
Shrubland	21.2	90°	2193	160	0.50	ENE	−0.6
						N	−2.0

<sup>a</sup> With respect to true north.

<sup>b</sup> Two aspects are listed for the forest site. The first applies to the northern one third of the flight line, while the second applies to the southern two thirds of the flight line.

Millington, New Jersey), and spectrometric surface irradiances matching Landsat TM bands 1–4 (Exotech Model 100BX-TM, Gaithersburg, Maryland), were also recorded at 100 Hz after anti-alias filtering, but were resampled and archived at 1 Hz for calculations of incident solar radiation, NDVI, APAR, and IR surface temperature. The spectrometer field of view was 15°, corresponding to surface footprints of 195–440 m<sup>2</sup> for the low-level flight data used in the present study. The surface IR temperatures assumed blackbody surface emittance and no absorption or emission by the intervening atmosphere.

[8] Pass-average values of net CO<sub>2</sub> uptake were calculated from the covariance of air vertical velocity and CO<sub>2</sub> mass mixing ratio, after first removing linear trends from both time series for each pass. The values of CO<sub>2</sub> uptake, NDVI, solar irradiance, APAR, and surface IR temperature used in the statistical analyses of section 3.2 were simple arithmetic means of the multiple, pass-average measurements during low-level flights across a particular site on a particular day (Table 1). The same flight lines were used for each site throughout the experiment.

[9] The pyranometer and spectrometer data used for NDVI and APAR were limited to times with the aircraft roll angle within 6° of wing-level, thus minimizing pyranometer detection of below-horizon radiation and keeping the spectrometer footprint close to a line directly beneath the aircraft. The pyranometer data were also corrected for aircraft roll, pitch, and heading and for solar azimuth and elevation [Bannehr and Glover, 1991].

[10] NDVI was calculated as

$$\text{NDVI} = \frac{r_4 - r_3}{r_4 + r_3}, \quad (1)$$

where  $r_4$  and  $r_3$  are the average spectral reflectances for the near-infrared and red wave bands 0.762–0.898  $\mu\text{m}$  and 0.629–0.687  $\mu\text{m}$ , respectively. The reflectance values were calculated from the near-infrared and red spectrometer irradiance values,  $I_4$  and  $I_3$ , as

$$\begin{aligned} r_4 &= \frac{I_4}{S_0 f_4} \\ r_3 &= \frac{I_3}{S_0 f_3}, \end{aligned} \quad (2)$$

where  $S_0$  is the incident solar irradiance and  $f_4$  and  $f_3$  are the fractions of  $S_0$  in the near-infrared and red wave bands, respectively. The numerical values of  $f_4$  and  $f_3$  (0.127 and 0.078, respectively) were averages from surface field measurements on 14 clear-sky days in May–September 1999 [Hunt et al., 2000], using a pyranometer (Eppley PSP, Newport, Rhode Island), two spectroradiometers (LICOR 1800, Lincoln, Nebraska; Analytical Spectral Devices Fieldspec Pro, Boulder, Colorado), and radiatively “white” reference surfaces (Labsphere Spectralon<sup>®</sup> panels, North Sutton, New Hampshire).

[11] The incident photosynthetically active radiation (PAR), or  $S_p$ , was calculated from the incident solar irradiance as

$$S_p = \varepsilon S_0, \quad (3)$$

with  $\varepsilon = 0.437$  based on the surface spectroradiometer measurements mentioned earlier. The fraction of  $S_p$  actually absorbed by the plants,  $f$ , was estimated from a linear relationship between  $f$  and NDVI,

$$f = a + b \text{NDVI}, \quad (4)$$

first described by Asrar et al. [1984] for cultivated wheat. This equation has been applied to a wide variety of vegetation classes (see review by Ruimy et al. [1994]). In the present study we assigned  $b = 1.25$  [Hunt et al., 2000], which is also the value reported by Asrar et al. [1984] and used by Ruimy et al. [1994] within a generalized model. Ruimy et al. [1995] used  $a = -0.025$ . We have used a slightly different value ( $-0.10$ ) based on snow-free winter AVHRR scenes of the grassland and shrubland sites [Hunt et al., 2000]. When combined, equations (3) and (4) yield the expression used for calculating APAR, or  $S_a$ , from the aircraft measurements,

$$S_a = 0.437 S_0 (1.25 \text{NDVI} - 0.10). \quad (5)$$

In the text, figures, and tables to follow, the APAR values have been converted from the pyranometer units ( $\text{W m}^{-2}$ ) to those of photon flux density ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) with the conversion factor used by Ruimy et al. [1995], i.e.,  $4.6 (\mu\text{mol m}^{-2} \text{s}^{-1})/(\text{W m}^{-2})$ .

### 3. Results and Discussion

#### 3.1. Site Homogeneity

[12] Evidence for homogeneity of plant cover along each aircraft transect can be gleaned from time traces of NDVI during cloud-free, low-level (60–90 m agl) passes. In general, these data showed NDVI as having small-scale variation superimposed on constant, pass-average values. Power spectral density plots for the 1-Hz NDVI traces indicated that most of the variance occurred at scales of about 2 km and smaller. As evidenced by nearly constant power spectral densities at scales  $\leq 2$  km, these smaller-scale variations appeared random in character, and could have originated from surface variation and/or instrument noise. Since APAR depends strongly on NDVI (equation (5)), the same pattern of small-scale variations also appears in time traces of APAR.

[13] Table 3 shows the ranges of pass-average NDVI and NDVI dispersion (standard deviation divided by mean) for midmorning, cloud-free passes along each flight line, grouped into the early, middle, and late growing season time periods. For each site, the mean NDVI values changed as expected through the growing season. Overall, the dispersion values ranged from 0.12 to 0.43 (standard deviation 12–43% of mean), with a general tendency for the dispersion to decrease as the growing season progressed.

[14] In addition, randomized transect and quadrat sampling along the entire shrubland flight line during three consecutive growing seasons indicated a high level of vegetative homogeneity for that site (W. K. Smith et al., Comparison of leaf-to-aircraft measurements of net CO<sub>2</sub> exchange in a sagebrush steppe shrubland, submitted to

**Table 3.** Ranges of the Mean and Dispersion Values for NDVI From Clear-Sky, Low-Level Passes Over Each Site

Site	Dates	Mean NDVI	NDVI Dispersion
Forest	May	0.38–0.46	0.35–0.43
	June–July	0.52–0.65	0.15–0.28
	Sept.	0.60–0.65	0.15–0.20
Grassland	May	0.25–0.29	0.19–0.25
	June–July	0.30–0.45	0.12–0.19
	Sept.	0.24–0.28	0.12–0.14
Shrubland	May	0.26–0.30	0.20–0.22
	June–July	0.24–0.41	0.15–0.23
	Sept.	0.14–0.26	0.14–0.25

*Journal of Geophysical Research*, 2001). Equivalent data were not available for the grassland and forest sites.

### 3.2. Relationships Between CO<sub>2</sub> Uptake and APAR

[15] Mean daytime net CO<sub>2</sub> uptake and APAR values for May–September 1999 (Figure 1) showed expected trends within the growing season, with some differences among the three sites. Forest APAR values were generally higher than all others, and remained high until the last day of measurements. In general, the patterns of net CO<sub>2</sub> uptake were similar for the grassland and shrubland, with uptake increasing to an early summer maximum, and then decreasing to zero, or near-zero, by early fall. The forest CO<sub>2</sub> uptake reached its maximum later than for the grassland and shrubland, as would be expected for the higher altitude of the forest site, but maintained higher values later in summer. As reviewed by *Smith* [1984, 1985], *Smith and Knapp* [1991], *Smith and Novak* [1991], and *Caldwell* [1985], there is considerable evidence that soil moisture remains

**Table 4.** Ranges of Daytime, Net CO<sub>2</sub> Uptake for Present Study and Other Sites<sup>a</sup>

Measurement Site	CO <sub>2</sub> Uptake, $\mu\text{mol m}^{-2} \text{s}^{-1}$	Reference(s)
Shrubland (present study)	0.2–7.6	—
Grassland (present study)	1.6–8.8	—
Tall-grass prairie	2.3–22.7	[Desjardins et al., 1992a, 1992b, 1995]
Forest (present study)	3.5–9.7	—
Boreal jack pine	2.2–6.8	[Desjardins et al., 1997]
Boreal black spruce	0–8.4	[Desjardins et al., 1997; McDermott and Kelly, 1995]
Boreal mixed forest	–1–9.8	[Oncley et al., 1997; Ogunjemiyo and Schuepp, 1997]

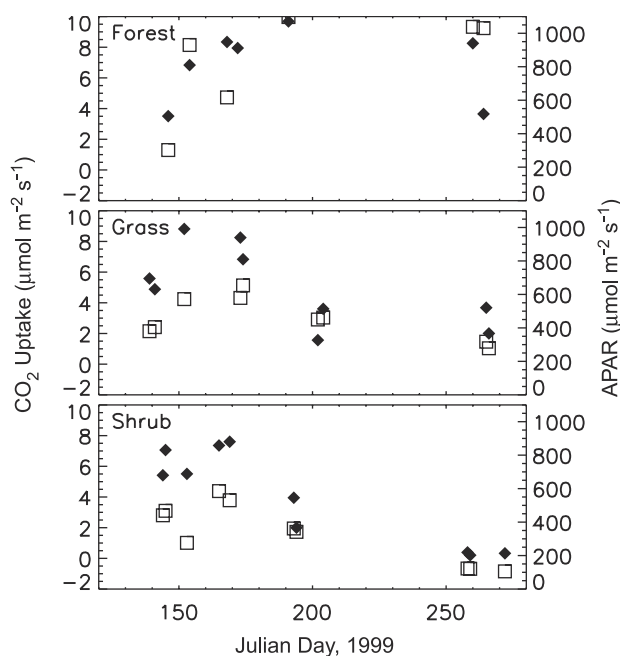
<sup>a</sup> The tall-grass prairie values are from project FIFE [Sellers et al., 1992]. The jack pine, black spruce, and boreal mixed forest values are from project BOREAS [Sellers et al., 1997].

higher for alpine forests than for shrublands and grasslands, and that soil moisture is more limiting to summer carbon uptake in the shrubland and grassland than the forest. The return of cold temperatures earlier in the fall dictates the shorter growth season found in these alpine/subalpine ecosystems. As also noted by *Smith and Knapp* [1991], the evergreen habitat of the forest ecosystem is an adaptation for maximizing carbon assimilation during this highly abbreviated, annual growth period.

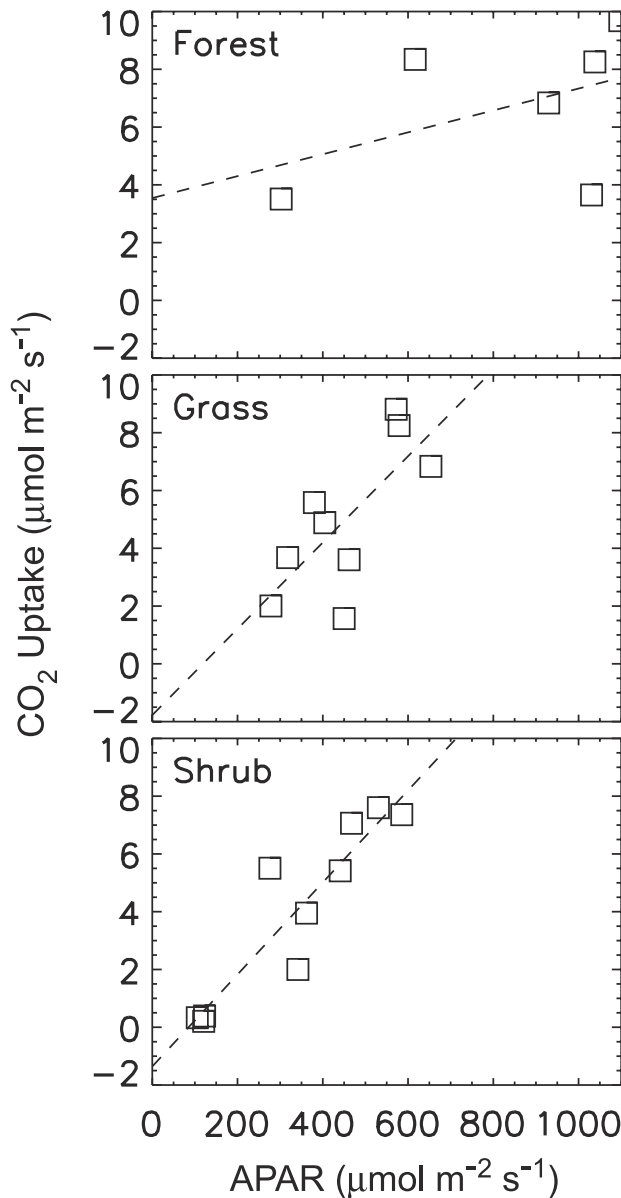
[16] The short-term variability superimposed on the seasonal trends of APAR (Figure 1) may be attributed to day-to-day differences in sky conditions, such as cloudiness, aerosol concentrations, and sun angle. The variability in CO<sub>2</sub> uptake may be attributed to short-term changes in site conditions (e.g., soil moisture and air and soil temperature), as well as statistical sampling uncertainties inherent in the eddy-correlation technique [Lenschow and Stankov, 1986].

[17] For two reasons the eddy covariance net CO<sub>2</sub> flux at aircraft flight level (60–90 m agl) was probably an underestimate of the net flux through a plane immediately above the plant canopy. First, the full response of the LICOR 6262 as used on the King Air was limited to frequencies less than about 2 Hz [Dobosy et al., 1997], so that CO<sub>2</sub> fluxes corresponding to eddies less than 80–90 m in scale were not fully sampled. Second, although measurements of fluxes during this project at heights ranging from 60–90 m agl to about 75% of the inversion height indicate little if any vertical divergence of CO<sub>2</sub> flux in the fully convective mixed layer, there may well have been some flux divergence in the layer between the flight level and the canopy. Such divergence would have resulted in the flight level fluxes being underestimates of the canopy top fluxes. Without corresponding flux measurements closer to the canopy, however, we could not quantify the resulting bias in the aircraft flux values.

[18] Table 4 compares the ranges of net, daytime CO<sub>2</sub> uptake from the present study with airborne measurements over other North American grasslands and forests. The range of May–September uptake values for the mixed-grass prairie of the present study was significantly less than that for a tall-grass Kansas prairie, as might be expected given the lower annual precipitation, cooler temperatures, smaller

**Figure 1.** Net, daytime CO<sub>2</sub> uptake (solid diamonds) and APAR (open boxes) over three mountain/high-plains landscapes from aircraft measurements over the period May–September 1999.





**Figure 2.** Scatter diagrams with linear regression lines for net, daytime CO<sub>2</sub> uptake versus APAR for the same three landscapes and measurement dates as in Figure 1.

plant biomass, and lower growth rates characteristic of mixed-grass versus tall-grass prairies [Coupland, 1950; Lauenroth, 1979; Larcher, 1995; Burke *et al.*, 1997; Lauenroth *et al.*, 1999]. In contrast, the range of CO<sub>2</sub> uptake values over the forest in the present study was similar to ranges measured for boreal jack pine, boreal jack pine, and mixed boreal forest.

[19] Two models were used by Ruimy *et al.* [1995], hereinafter referred to as R95, to examine over 1300 data sets relating CO<sub>2</sub> flux and APAR over a variety of vegetation classes,

$$F_c = \alpha Q - R \quad (6)$$

$$F_c = \frac{\alpha Q F_\infty}{\alpha Q + F_\infty} - R, \quad (7)$$

where  $F_c$  is the net downward CO<sub>2</sub> flux density through a plane above the canopy,  $Q$  is the photosynthetically active photon flux density (PPFD),  $F_\infty$  is the net downward CO<sub>2</sub> flux at saturating  $Q$ ,  $\alpha$  is the apparent quantum yield, and  $R$  is the ecosystem respiration rate.

[20] Only two of the data sets used by R95 were from aircraft. The rest were either from “instantaneous” micrometeorological measurements (about two thirds) or enclosure measurements (about one third). In general, R95 found that CO<sub>2</sub> uptake computed from micrometeorological measurements was nonlinearly related to APAR, but not as nonlinear as the data from gas-exchange enclosures. Our above-canopy aircraft measurements should be most similar to the micrometeorological data. R95 noted that both of the aircraft-based data sets they examined (one for wheat [Desjardins, 1991] and one for a mixed conifer/broadleaf forest [Desjardins *et al.*, 1985]) were best described by the linear model (equation (6)). In addition, R95 noted that extrapolating the measurements they reviewed to longer timescales tended to linearize the relationship between CO<sub>2</sub> uptake and APAR. The multipass averages reported here represent longer time periods than the “instantaneous” enclosure and micrometeorological data compiled by R95.

[21] Further insight into the suitability of the linear model to the present study was gleaned from an aircraft-based study by Cihlar *et al.* [1992], hereinafter referred to as C92. Their data came from repeated, 75-km, low-level flights across a mixed agricultural area in central Kansas, and were used to examine relationships between aircraft-level net CO<sub>2</sub> flux and NDVI for 25 3-km segments along the flight line. For a single pass, i.e., for a particular day, the flux-NDVI relationships appeared linear. For the composite data set (4 days from late June to early October) the flux-NDVI relationship was nonlinear. As noted by C92, however, the nonlinearity stemmed from the measurements on a single day (mid-July), which also had the highest NDVI values ( $\geq 0.7$ ), leading C92 to suggest that the nonlinearity may have resulted from NDVI saturation. The remaining data, all with NDVI  $< 0.7$ , appeared to have a linear flux-NDVI relationship. The NDVI values for the present study were all  $\leq 0.65$ , with maxima of 0.65, 0.45, and 0.39 for the forest, grassland, and shrubland, respectively, and thus all within the range of linear flux-NDVI relationships noted by C92.

[22] Given these observations, i.e., given the increased linearity for above-canopy measurements (R95), the linearity of aircraft data examined by R95, and the linearity for aircraft data with NDVI  $< 0.7$  examined by C92, plus the fact that the present aircraft study did not include direct measurements of either respiration rate or net CO<sub>2</sub> uptake at saturating APAR, we chose to examine only the applicability of the linear model from R95 (equation (6)) to our measurements.

[23] When net CO<sub>2</sub> uptake is plotted against APAR for each site (Figure 2), much of the seasonal variation noted in Figure 1 is translated to apparent linear relationships for the grassland and shrubland data, but not a significant linear relationship for the forest data. Results from linear regressions of CO<sub>2</sub> uptake versus APAR for each site are listed in the first group of entries in Table 5. As shown, regressions for both the grassland and shrubland had F-statistics that were significant at the 0.025 level or better, while that for

**Table 5.** Results of Single Linear Regressions of CO<sub>2</sub> Uptake Versus APAR, Single Linear Regressions of CO<sub>2</sub> Uptake Versus IR Surface Temperature, and Multiple Linear Regressions of CO<sub>2</sub> Uptake Versus APAR and IR Surface Temperature for Each Site, May–September 1999<sup>a</sup>

Independent Variable	Site	$r^2$	$r_0^2$	$r_1^2$	$m_0$	$m_1$	$b$	$k$	$n$	$F_s$	Significance
APAR	Forest	0.24	—	—	0.0038	—	3.54	1	7	1.58	0.25
	Grass	0.53	—	—	0.0149	—	-1.78	1	9	7.93	0.025
	Shrub	0.85	—	—	0.0159	—	-1.36	1	10	45.2	0.001
$T_{IR}$	Forest	0.66	—	—	—	0.315	-83.7	1	7	9.60	0.025
	Grass	0.02	—	—	—	-0.130	44.5	1	9	0.143	>0.5
	Shrub	0.11	—	—	—	0.126	-33.6	1	10	0.961	0.5
APAR and $T_{IR}$	Forest	0.66	0.24	0.66	0.0005	0.313	-83.3	2	7	3.84	0.1
	Grass	0.56	0.53	0.02	0.0150	-0.144	41.9	2	9	3.75	0.1
	Shrub	0.90	0.85	0.11	0.0184	-0.099	27.3	2	10	30.0	0.001

<sup>a</sup>The first column lists the independent variable(s) for each regression;  $r^2$  is the square of the correlation coefficient for the single correlations and the square of the joint correlation coefficient for the multiple regression;  $r_0^2$  and  $r_1^2$  apply to APAR and  $T_{IR}$ , respectively, within the multiple regressions. The definitions of  $m_0$ ,  $m_1$ , and  $b$  may be seen in the full regression equation,  $y = m_0 \times \text{APAR} + m_1 \times T_{IR} + b$ ;  $k$  is the number of independent variables;  $n$  is the number of observations;  $F_s$  is the F-statistic with  $k$  and  $n - k - 1$  degrees of freedom and a corresponding level of significance as shown in the last column [Montgomery and Peck, 1992].

the forest was significant only to 0.25. Thus the linear model was strongly suggested for the grassland and shrubland data, but was not suggested for the forest data.

[24] As indicated by R95 and others [Ruimy *et al.*, 1994; Liu *et al.*, 1999; Hunt *et al.*, 1996, 2000], respiration should be an important component in above-canopy flux-radiation relationships, and potentially could account for the lack of a linear relationship for the forest as well as for some of the scatter in the data for all three sites. Knowing that respiration can vary with environmental conditions, including canopy and soil temperature (R95), we thought it would be informative to examine multiple linear regressions of CO<sub>2</sub> uptake versus APAR and an environmental variable related to respiration rate,  $R$ , in equation (6), in particular one which could be approximated from aircraft measurements. For that purpose the surface IR temperature,  $T_{IR}$ , was used to estimate canopy temperature.

[25] Note that the use of multiple regressions in this context implies neither that there is necessarily a linear relationship between above-canopy net CO<sub>2</sub> uptake and canopy temperature, nor that canopy temperature is the only or most important environmental variable besides APAR determining net CO<sub>2</sub> uptake. Furthermore,  $T_{IR}$  estimates of canopy temperature will include errors when the soil surface is “visible” through a sparse canopy.

[26] Scatter diagrams of CO<sub>2</sub> uptake versus  $T_{IR}$  for each site are shown in Figure 3. Results from linear regressions of CO<sub>2</sub> uptake versus  $T_{IR}$  are listed as the second group of entries in Table 5. For these regressions, only the forest data had an F-statistic that was significant at the 0.025 level, suggesting a linear relationship. In contrast, the F-statistics for the grassland and shrubland data do not suggest a linear relationship between CO<sub>2</sub> uptake and  $T_{IR}$ .

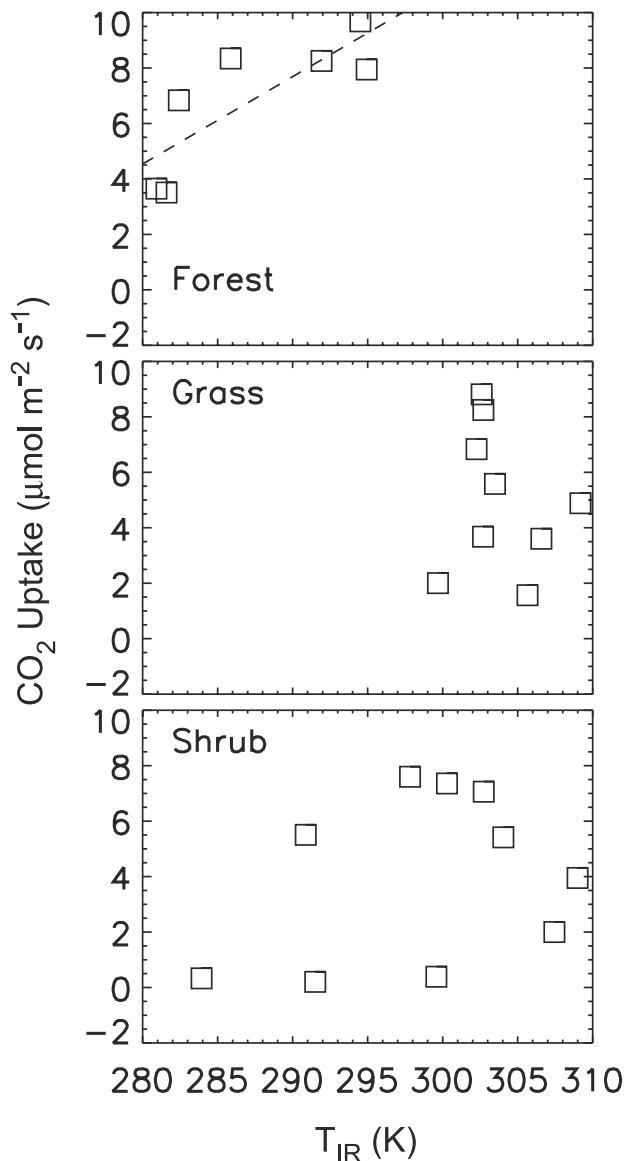
[27] Combining all three regression variables, the results of multiple linear regressions for CO<sub>2</sub> uptake as a function of APAR and  $T_{IR}$  are shown as the last group of entries in Table 5. For these calculations the F-statistics strongly suggest a multiple linear relationship for the shrubland data, but only weakly suggest a multiple linear relationship for the forest and grassland data.

[28] In addition to examining the F-statistics, one can also compare the  $r^2$  values (squares of correlation coefficients) for the regressions (Table 5). For all three sites, the joint  $r^2$

for the multiple regressions were greater than those for the simple regression of CO<sub>2</sub> uptake against APAR, with a significant increase for the forest data (0.24–0.66) and only small increases for the grassland data (0.53–0.56) and shrubland data (0.85–0.90). Equally important, as shown by the  $r^2$  values for each independent variable in the multiple regressions, the multiple regressions for the grassland and shrubland data were dominated by the strong linear relationships between CO<sub>2</sub> uptake and APAR, while the multiple regressions for the forest data were dominated by the strong linear relationship between CO<sub>2</sub> uptake and  $T_{IR}$ .

[29] Overall, then, the regression analyses presented here suggest that APAR would be a strong predictor of net, daytime CO<sub>2</sub> uptake for the grassland and shrubland landscapes. In contrast, these results also suggest that APAR would be a poor predictor of net, daytime CO<sub>2</sub> uptake over the forest. Moreover, regressions incorporating  $T_{IR}$  suggest that respiration may be more important than APAR in determining net CO<sub>2</sub> uptake over the forest. This latter result is consistent with ecophysiological measurements showing that high-elevation conifer forests may have reduced carbon assimilation on days with large values of incident PAR, because such days occur most frequently following clear, cold nights that can occur throughout summer [Smith and Knapp, 1991; Anthoni *et al.*, 1999]. The lack of a positive linear relationship between CO<sub>2</sub> uptake and APAR for the forest may also be related to observations that on cloudy/partly cloudy days there will be less full-shadow (numbra) volume in the conifer canopy, exposing the canopy to more evenly distributed, diffuse radiation that is closer to photosynthetic saturation, while avoiding possible photoinhibition under higher sunlight levels (especially following near-freezing nights) [Roderick *et al.*, 2001]. Thus, as has been observed for a conifer forest (Scots pine) in Finland [Baldocchi *et al.*, 2001], greater carbon assimilation by the forest might be expected on cloudy and overcast days compared to clear days with high irradiance levels.

[30] Drawing further on the regression results, it should be noted that for the grassland data of the present study, the slope for CO<sub>2</sub> uptake versus APAR ( $m_0 = 0.015$  in Table 5) agreed closely with that found by R95 for C3 grasslands (0.017). Since the forest data of the present study did not



**Figure 3.** Scatter diagrams with linear regression lines for net, daytime CO<sub>2</sub> uptake versus surface infrared temperature for the same three landscapes and measurement dates as in Figure 1.

show a linear relationship between CO<sub>2</sub> uptake and APAR, the slopes were not compared with those found by R95. R95 did not include shrubland data.

#### 4. Summary

[31] At the landscape scale, linear relationships between CO<sub>2</sub> uptake and APAR, as modeled by R95, appeared valid for grassland and shrubland landscapes observed in southeastern Wyoming, with increasing APAR corresponding to increasing CO<sub>2</sub> uptake. Over a nearby, high-altitude conifer forest, changes in CO<sub>2</sub> uptake had very little correspondence to changes in APAR. Simple multiple linear regressions of CO<sub>2</sub> uptake versus APAR and an estimate of canopy temperature implied that respiration may have been more important than APAR in determining the net uptake for the conifer forest. The regression slope for CO<sub>2</sub> uptake

versus APAR for the grassland data agreed quite well with that compiled for C3 grasslands by R95.

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